Movement Variability is Processed Bilaterally by Inferior Parietal Lobule

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Robots with artificial intelligence have made enormous progress in solving complex cognitive tasks, but when it comes to learning and executing coordinated, smooth, and complex movements, humans and animals still excel. To ensure consistent skilled movements, the motor system needs to learn how to control and exploit movement variability.

While some movement variability is “noise” that results from stochastic neural and muscle activity and can reduce task success (Faisal et al., 2008), other movement variability does not harm performance. For instance, when one is playing tennis, multiple combinations of movement of the shoulder, elbow, and wrist joint can result in a successful hit. This abundance of possible movements constitutes “task-irrelevant” motor variability, so-called because it does not affect successful task completion; the motor system can, however, exploit task-irrelevant variability to optimize motor performance (Sternad et al., 2011; Wolpert et al., 2011). Moreover, it can learn through such variability that certain body positions minimize the impact of unexpected perturbations and how to flexibly switch to a different movement to compensate for muscle fatigue or injuries (Latash, 2012). Understanding the neural control of both forms of movement variability is hence central for the study of human movement control in health and disease.

Non-invasive brain stimulation can probe neural sources of motor variability, but current techniques are limited by relatively poor control over perturbation site and intensity (Siebner et al., 2009; Horvath et al., 2014). Invasive recordings from implanted electrodes allow researchers to correlate movement kinematics with neural activity in small populations of neurons (Churchland et al., 2006; Kaufman et al., 2014), but these methods are too invasive for use in healthy humans and they do not allow measurement of simultaneous neural activity from many sites in the brain. In contrast, non-invasive neuroimaging with fMRI can record the neural correlates of motor variability across the brain. The blood-oxygen-level dependent (BOLD) signal captured by fMRI reflects the ratio of oxygenated to deoxygenated blood, which largely depends on energy consumption by local neural populations and resulting increases in local blood flow due

to neurovascular coupling, but it is also affected by other, non-neural factors. Potential methodological concerns for fMRI include the slowness of vascular responses to neural activity and the presence of non-neural variability (e.g., heart-beat, breathing, and head motion) that can confound measurements. However, by modelling the delay and correcting for non-neural noise, fMRI signals can reveal brain activity during fast-evolving behavior like arm reaches.

In a recent study, Haar et al. (2017b) report intriguing correlations between inter-trial neural variability (measured with fMRI) and inter-trial movement variability during arm reaches. They instructed 32 healthy adults to perform out-and-back reaching movements to near and far target locations using a pen stylus on a digital drawing tablet while fMRI was recorded. No visual feedback about the endpoint position or trajectory was provided during or after movements to minimize neural variability stemming from visual feedback. Hence, subjects did not know whether their reaches were accurate.

The authors quantified the trial-by-trial neural variability (fMRI variability around individual mean response) and variability in reach extent, direction, and velocity for each subject, and they tested whether subjects exhibited consistent magnitudes of neural variability in multiple cortical motor regions of interest (ROIs) during reaches to different targets and during reaches with each arm. Neural variability in several motor and pre-motor ROIs in each hemisphere were correlated across reaches to different targets by the right arm (Fig 5A) and by the left arm (Fig 5B). In addition, variability in the premotor cortex, superior parietal lobule, and supplementary motor area in each hemisphere was correlated for right and left arm reaches (Fig. 5C). Taken together, these results indicate that subjects exhibited consistent magnitudes of neural variability regardless of the arm used to perform the movements or the target to which they reached.

To study the neural control of movement variability, Haar et al. tested whether neural variability was correlated with any of their three measures of movement variability: reach extent, direction, or velocity. A link between neural variability and movement variability was found bilaterally in the inferior parietal lobule (IPL), which explained about

24% of between-subject differences of variability in movement extent (Fig 6). This finding was corroborated by an exploratory searchlight analysis of the cortical surface. The searchlight identified additional clusters in a medial area of the superior parietal lobule (SPL), the precuneus (Fig 7). These results extend previous reports of effector-invariant encoding of movement directions (Haar et al., 2017a) to effector-invariant encoding of movement variability in the IPL and SPL.

These results raise a question: why does the motor system involve both hemispheres in processing movement variability of either arm? One possible reason is that the motor system integrates knowledge of movement variability across arms to maximize error reduction and thereby facilitate motor learning. Movement extent variability is critical for task success and provides a crucial learning signal that has been extensively studied in perturbation experiments (Wolpert et al., 2011). Encoding movement variability across both arms may come at a higher computational cost for the motor system, but it allows both hemispheres to learn from errors made by either limb. Transfer of learning between hands and limbs has been described in simple and complex motor tasks (Lee et al., 2010; Dickins et al., 2015), and the IPL and precuneus may facilitate this process. Furthermore, effector-invariant encoding of reaching directions has been shown in an identical task for several ipsi- and contralateral cortical motor areas, but barely for the IPL (Haar et al., 2017a). Together, these findings suggest that the IPL might mainly encode movement variability during reaching when no task feedback is provided. However, the function of the IPL (and precuneus) in this task setting remains an open and intriguing question.

Another interpretation for the observed bilateral IPL and precuneus activity relates to processes that were emphasized in the present experiment because of the lack of visual task feedback. While the interpretation above relies on the role of the IPL in motor planning and preparation (Cohen and Andersen, 2002), these processes typically require knowledge of task success from previous motor actions. Without visual feedback about task success, however, motor planning in the present experiment was limited. As a result, two other processes likely interacted to guide the reaches subjects

performed in the experiment: 1) shifting attention towards the action space (informed by reappearing target locations), and 2) monitoring joint configurations (informed by proprioception). Haar et al's findings are in line with the expected neural bases of these processes: the IPL is critically involved in processing and attending to peripersonal space (Fogassi and Luppino, 2005), i.e., the action space that immediately surrounds the body, and the IPL's role in spatial attention has previously been demonstrated (Mattingley et al., 1998). Similarly, the precuneus – which receives input from premotor regions and the IPL (Margulies et al., 2009) – is also involved in shifting spatial attention between different target locations in the absence of visual feedback (Wenderoth et al., 2005) and updating postural representations of the upper limb during reaching (Pellijeff et al., 2006). The specific experimental design used in the present study likely recruited these IPL and precuneus functions; therefore, it remains to be tested whether these regions also process movement variability when visual feedback is provided.

Another open question is which brain regions process task-irrelevant variability. The stylus pen recorded movement data only from the tip and thus only quantified task-relevant variability, but the whole movement required complex coordination in multiple joints of the arm. Therefore, the same position of the stylus tip may have been executed using many different joint configurations across trials, leading to task-irrelevant variability. While task-irrelevant joint variability tends to be larger than task-relevant endpoint variability for healthy subjects (Wolpert et al., 2011), high task-relevant endpoint variability dominates when joint control is impaired, e.g. due to stroke (Cirstea and Levin, 2000). Neural correlates of joint-based control over reaching directions for an identical task included activity in the IPL and SPL (Haar et al., 2017a). Extending this work to task-irrelevant variability could yield valuable insights into the neural mechanisms contributing to both the benefits (Sternad et al., 2011; Wolpert et al., 2011; Latash, 2012), and challenges (Cirstea et al., 2003) that arise from movement variability in movement control.

Haar et al. demonstrate that humans show consistent magnitudes of neural variability across hemispheres regardless of the movements performed. Additionally, they report

that bilateral IPL, a key region in motor planning, processes movement extent variability irrespective of arm use. This suggests that both hemispheres cooperate in controlling movement extent variability, a metric critical for task success and motor learning. However, the function of IPL, and the generalizability of findings to tasks that involve visual feedback and quantify task-irrelevant variability remains to be tested.

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